THE TARSUS OF THEROPOD DINOSAURS

By

Samuel P. Welles & Robert A. Long

University of California Museum of Paleontology, Berkeley

(With 13 figures)

Contents

Introduction

The theropod tarsus is a very highly evolved structure, and the investigation of its origin and development is a most intriguing subject. As with most such studies, each new discovery reveals new unsolved problems, most of which cannot be pursued because they diverge too far from the main topic of research. Our interest in this rather specialized subject was aroused by the tarsi of two individuals of *Dilophosaurus*, both in a fine state of preservation. We have long searched for theropods that might show relationship to *Dilophosaurus*. This led us to a comparative study of theropod tarsi and an inquiry into the origin of this peculiar mechanism. We have tried to limit our thoughts to the tarsus, but we must caution the reader that, consciously or unconsciously, our conclusions have probably been influenced by our knowledge of other parts of the skeleton.

General Evolution of the Reptilian Tarsus

The theropod hind limb was derived from that of a quadrupedal archosaur or protoarchosaur, probably by or in the early Triassic. In the ancestral forms the femur is essentially horizontal, projecting laterally and swinging forward and backward about the knee. It has been customary to think of the leg as rotating in the acetabulum, and this is indeed the condition in the recovery stroke. However, once the foot becomes planted in its forward position the whole action is reversed and the foot becomes the pivot about which the epipodials and propodial revolve. We therefore think of a fixed pes with the limb lever

Ann. S. Afr. Mus. **64**, 1974: 191–218, 13 figs.

Relationships of theropod tarsi

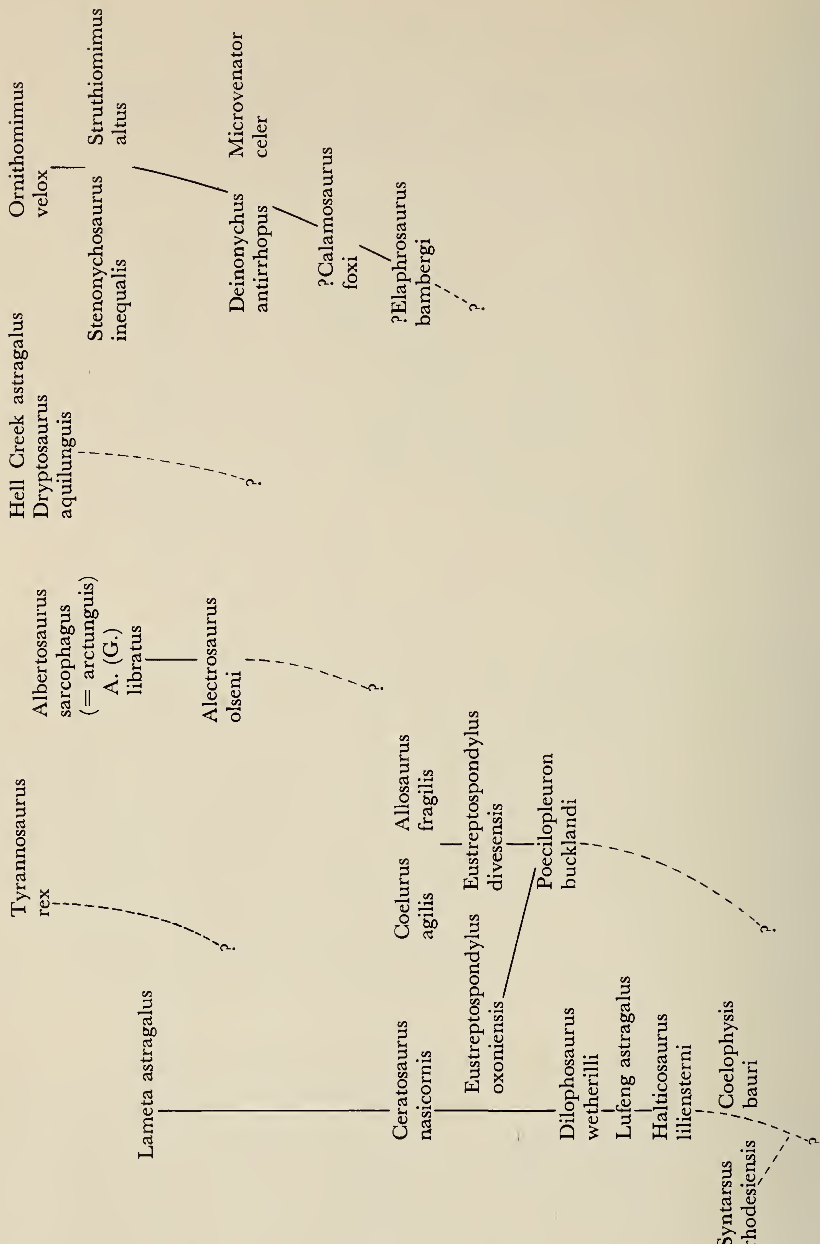

Table of indices and measurements of theropod tarsi

	H:B index from straight line across bottom of astragalus	H:B index including calcaneum	Dip of medial edge of dorsal process	Breadth of astragalus in mm.	Breadth of astragalus plus calcaneum in mm.
Tyrannosaurus rex	86	—	10	372	—
Hell Creek LACM	—	—	—	196	—
Ornithomimus velox	154	123	60	52	65
Albertosaurus sarcophagus (Dryptosaurus incrassatus, cfd.)	97	—	52	248	—
Albertosaurus sarcophagus, cfd. (A. arctunguis)	123	—	—	216	265
Struthiomimus altus Lamb 1902	174	154	—	129	146
Albertosaurus libratus (Gorgosaurus l.)	148	128	67	212	246
Alectrosaurus olseni	150	129	55	120	141
Deinonychus antirrhopus	142	129	72	59	65
Microvenator celer	190	—	75	22,3	—
Calamosaurus foxi estimated	132	—	—	25	—
Coelurus agilis	78	—	—	74	—
Allosaurus fragilis cast	87	77	50	185	208
A. f. juv. cast	104	93	—	98	110
Ceratosaurus nasicornis, type	—	46	35	—	130
C. n., type, left, YPM	—	45	—	—	118
C. ?n. UUVP 5682	—	49	—	—	147
C. ?n. UUVP 5681	—	42	—	—	175
Elaphrosaurus bambergi	—	100	—	88	—
?Eustreptospondylus Dives. Cuvier's	86	—	38	120	—
Eustreptospondylus oxoniensis	71	—	32	87	—
Poecilopleuron bucklandi	75	—	60	148	—
Dilophosaurus wetherilli UCMP 37302	77	61	27	91	—
D. w., cfd. UCMP 37303 estimated	58	48	20	—	114
Lufeng astragalus	—	53	18	—	157
Halticosaurus liliensterni	65	53	11	65	79
Syntarsus rhodesiensis	—	49	12	—	20
'Coelurosaur' Bonaparte est.	60	60	—	15	15
Coelophysis bauri	—	65	20	—	23

acting from this base. It functions by lifting the lower leg and foot, swinging them forward in a nearly horizontal arc centred at the acetabulum, or even farther inward if there is a concomitant sigmoid flexion of the vertebrae. This plants the foot in a forward position. Next there is a transfer of part of the body weight to this new base and its epipodial pillar. Then follows a horizontal rotation of the femur about the knee, atop the more or less fixed epipodials, which moves the acetabulum forward. At the same time the body weight is held above the ground, or at least lifted enough to be slid forward. The mechanics are first to lift and swing the epipodium and foot forward, then to reverse the forces and lift the body on this new fulcrum and propel the body forward.

As described by Schaeffer (1941: 412) in the salamanders, the propulsion phase begins immediately on the contact of the plantar surface of the foot with the ground. The recovery phase starts with the dorsal surface of the foot turning laterally into a vertical position. The crus is carried forward as an extension of the femur until just in front of a position at right angles to the body. The last movements involve a flexion of the knee, the extension of the foot and its rotation into a horizontal plane. This kind of limb movement, Schaeffer noted, was probably used by the smaller primitive amphibians. He went on to point out that Gregory & Camp (1918) had described the Permian reptile knee as permanently bent, and he thought that the heavier labyrinthodonts must have had similarly permanently flexed knees.

Broom (1921) presented the first general review of the reptilian tarsus, tracing it from the early Permian labyrinthodont *Trematops milleri* up into the therapsid reptiles. While he did include some other reptiles, he did not discuss the thecodonts or the dinosaurs. He noted Gegenbaur's pioneer work and used his terminology.

Schaeffer (1941) also began with the tarsus of *Trematops*. From this he derived that represented by the early Permian cotylosaur *Labidosaurus*, and this became the ancestral pattern for later tetrapods. He found these later forms to have three divergent kinds of tarsi. His type I is a retention of the primitive pattern or its modification into an aquatic paddle as seen in the marine reptiles. The movement is originally infratarsal. Type II developed a mesotarsal joint with various specializations. Here the astragalus and calcaneum are functionally part of the epipodium, except in the crocodiles and most thecodonts. This joint developed in the Chelonia and, independently, in the lines leading from the Eosuchia, although not present in the Eosuchia themselves. In this type the distal tarsals become reduced. Type III is that leading to the epitarsal joint of the pelycosaurs, therapsids, and mammals.

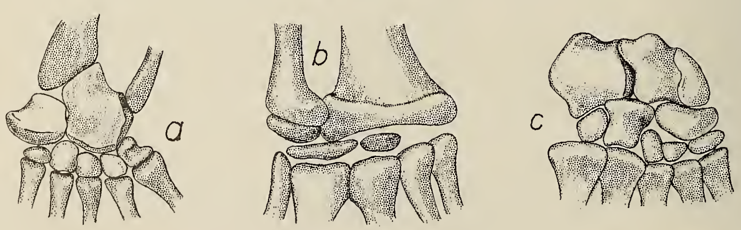

Fig. 1. Reptilian tarsi.
a, type I, *Mesosaurus*; b, type II, *Plateosaurus*; c, type III, *Youngina*. Modified from Schaeffer 1941, fig. 11, not to scale.

Schaeffer's type II is, of course, the one that interests us. He wrote (p. 446), 'the final stage in the perfection of the mesotarsal joint is found in the Saurischia, Ornithischia, Aves, and Pterosauria'. Here the astragalus and calcaneum have become depressed and the distal tarsalia are reduced to two or three. The astragalus and calcaneum may become fused, and are attached to the tibia and fibula. The distal surfaces of the astragalus and calcaneum become rounded into a transverse hemicylinder. At the same time the femur develops a medial head and the tibia becomes the prominent weight-bearer, with the fibula much reduced. In the theropods the tibia develops a distal lateral flange that extends behind the fibula. It also develops a sulcus on the anterolateral distal face, into which fits the ascending process of the astragalus.

Since the publication of Schaeffer's work evidence has accumulated to indicate that there are at least two basic kinds of tarsi in the archosaurs. The first is the crocodiloid tarsus with its intertarsal movement, having the astragalus locked to the tibia and the calcaneum locked to the pes. Movement between the astragalus and calcaneum is rotation about a horizontal axis. The second kind has both astragalus and calcaneum locked to the epipodials, or at least moving with them, and the movement is a hinge below these proximal tarsals. We can therefore expand Schaeffer's classification to include II A, the crocodiloid tarsus, and II B, the dinosauroid tarsus.

The Pivot Tarsus of the Crocodiloids

The crocodiloid tarsus probably had as its ancestral stages those of the amphibians, cotylosaurs, and eosuchians. The movement was originally one of flexion, but later, in the thecodonts developed into a pivot, a rotation of the crus on or through the tarsus as the body moved forward. Some of this rotation was absorbed in the knee but much or most of it involved the crurotarsal joint. This pivot joint is found in such crawling forms as aetosaurs and crocodilians where the tibia can rotate upon the astragalus. Especially in the aetosaurs, this resulted in spiral articular surfaces between the two bones. This prohibited any hinge motion between tibia and astragalus and caused them to act as a unit so that the hinge developed between the astragalus and the distal tarsals on the inside, and the fibula and the calcaneum on the outside.

The astragalus in this foot was so named as early as Cuvier (1836, 9:207). Gegenbaur (1864: 88) first demonstrated that the bone was a composite of tibiale, intermedium and centrale, based on his embryological studies. Rabl (1910: 242) also found it to originate in three embryonic centres and so called it the 'tritibiale' This was later beautifully demonstrated in the cotylosaur *Captorhinus* by Peabody (1951: 340). Steiner, however, (1934, *fide* Krebs, 1963: 92) derived the astragalus from four embryonic centres representing the intermedium, proximal centrale, distal tibial centrale, and tibiale. Gegenbaur (1864: 92) noted the unique character of the crocodile foot and wrote 'Der Calcaneous bewegt sich mit dem Unterschenkel fester verbundene Astragalo-

Scaphoideum nur mit dem Unterschenkel sich bewegt'. He named this kind of joint, with the movement between the astragalus and calcaneum 'intertarsal' (p. 93). Schaeffer (1941: 442) considered the crocodiloid tarsus unique, yet noted the similarity between that of *Protosuchus* and *Aetosaurus*. He analysed the motion as a 45° rotation of calcaneum on astragalus, the latter immobile and functionally united with the crus, while the calcaneum moved as a part of the foot.

This crocodiloid intertarsal joint is widespread among the thecodonts. Ewer (1965: 426) described an ideal pre-crocodiloid ankle in the Olenekian *Euparkeria* and demonstrated that its astragalus functions as a unit with the tibia, while the calcaneum is attached to and works with the foot. This is the same crocodiloid structure that was described by Gegenbaur (1864: 92) in the crocodile but is more primitive in lacking the peg-and-socket joint between astragalus and calcaneum that is found in the crocodiles. Although Ewer considered *Euparkeria* to be the earliest example of such a tarsus, a calcaneum was referred to *Wangisuchus tzeyii* Young (1964: 179, fig. 60 A) which has a well-defined astragalar sulcus, head, and tuber. This is from the Ehrmaying Series (Olenekian), the same age as *Euparkeria*, but has a more advanced, truly crocodiloid structure.

A possible mechanical explanation for the retention of this peculiar tarsus in the living crocodiles is that these reptiles have two distinct gaits. In the slow gait the animal crawls with the body close to the ground. The femur is horizontal and a certain amount of rotation of tibia on astragalus is required. Also, the fibula must be free to rotate on the calcaneum, which explains the ball-on-ball articulation between the two bones. In the fast gait the body is held high off the ground, the femur moves in a plane that dips about 60° laterally, and the astragalus is locked to the tibia. The movement then becomes entirely hinge, or dorsoflexion, between the metatarsals and the unit composed of tarsalia, astragalus and tibia on the inside, and the calcaneum and fibula on the outside.

The Hinge Tarsus of the Dinosaurs

The dinosaur tarsus with its mesotarsal hinge is very different from the tarsus discussed above. Krebs (1963: 91), Ewer (1965: 426), and Bonaparte (1969: 474) each maintained, and we agree, that the mesotarsal joint cannot be derived from the intertarsal joint. Furthermore, as noted by Bonaparte, the twisted tibia of the Triassic dinosaurs is very different from the straight tibia of the pseudosuchians. Attridge (in Bonaparte) pointed out the association of the twisted tibia with this mesotarsal dinosaur articulation. Present evidence indicates an entirely separate origin for the dinosaur mesotarsal hinge.

The mesotarsal joint is also correlated with an inturned head of the femur and with the femur moving in a nearly vertical plane. The mesotarsal joint limits the movement to a parasagittal plane and is an adaptation to bipedal locomotion. However, bipedal locomotion may also develop in the crocodiloid tarsus, as in *Saltopus*. Furthermore, Dr Alan Leviton of the California Academy of Sciences informs us that several of the desert lizards, including *Callisaurus* and *Crotaphytus* can run bipedally with the femur in a vertical plane and the feet under the body. This is to say that although the mesotarsal joint is a bipedal adaptation, bipedalism may also develop in reptiles with other kinds of tarsi.

The earliest of the mesotarsal ankles are in the two ?Anisic genera *Lagerpeton* and *Lagosuchus* described by Romer (1971, 1972). *Lagerpeton* has a short astragalus, fused to the calcaneum, and with a dorsal process up the posterior side of the tibia. This is a unique arrangement among dinosaurs, for in all other known forms the dorsal process develops up the anterior face of the tibia. The question naturally arises as to whether *Lagerpeton* can truly be included in the dinosaurs. *Lagosuchus* has a quite different tarsus in that the astragalocalcaneum is much longer, there is no dorsal process, and there is a small posterior spur on the calcaneum. These two reptiles are quite different from each other and neither shows any direct relationship to later archosaurs.

Our studies indicate that the theropod tarsi can be grouped into five rather distinct kinds:

1. Ceratosauroid—the astragalus with a low dorsal process that is sunk into the tibia, and a large calcaneum that is closely applied to or fused with the astragalus. Late Triassic to late Cretaceous. *Ceratosaurus*, *Coelophysis*, *Dilophosaurus*, *Halticosaurus*, Lameta astragalus, Lufeng astragalus, *Syntarsus*.
2. Allosauroid—the astragalus with a moderately high dorsal process that is set into the anterior face of the tibia and yet has a free horizontal medial component. The medial condyle is large and the medial end rounded. A deep upper horizontal groove develops at the anterior base of the dorsal process and a deep lower horizontal groove across the face of the condyles. The calcaneum is free and large, and in *Allosaurus* develops a medial tongue and two pits to fit the astragalus. Middle Jurassic to late Jurassic. *Allosaurus*, *Coelurus*, *Eustreptospondylus*, '*Megalosaurus bucklandi*', Phillips, *Poecilopleuron*.
3. Albertosauroid—the astragalus with a high dorsal process that is applied to the entire anterior and anterolateral faces of the tibia. A deep upper horizontal groove develops above the condyles. This is interrupted laterally by a ventrolateral buttress to the lateral condyle. The condylar surface does not develop the lower horizontal groove. The calcaneum is reduced and free from the astragalus. Late Cretaceous. *Albertosaurus*, *Alectrosaurus*, *Dryptosaurus*, Hell Creek astragalus.
4. Ornithomimoid—the astragalus with an extremely high dorsal process that is applied to the entire anterior face of the tibia. The calcaneum is reduced or absent. Late Jurassic to late Cretaceous. ?*Calamosaurus*, *Elaphrosaurus*, *Microvenator*, *Ornithomimus*, *Stenonychosaurus*, *Struthiomimus*.
5. Tyrannosauroid—the astragalus with a high, wide dorsal process. The upper horizontal groove shallow and restricted to the medial half. No lower horizontal groove, but a large oval foramen in the centre of the anteroventral condylar face. The medial condyle high, its dorsal border sloping steeply ventromedially; the lateral condyle weakly developed.

These five kinds of tarsi will be described in the following paragraphs.

THE CERATOSAUROID TARSUS

Coelophysis bauri from the upper Chinle Formation of New Mexico, was previously thought to have an astragalocalcaneum without a dorsal process, but preparation of the tarsus at the American Museum of Natural History (block 5) has revealed a well-developed dorsal process on the astragalus. This was not known to Dr E. H. Colbert and so was not indicated in the figure published by Raath (1969, fig. 6d) on information from Colbert. Dr Colbert is preparing a monograph on *Coelophysis* but he has kindly consented to our advance publication of this information. This astragalocalcaneum is skewed anterointernally, has a maximum breadth of 23 mm anteriorly and 22 mm posteriorly. It is 11 mm long internally and 12 mm externally. The dorsal process is 15 mm high above the plane of the distal condyles, yielding an H:B

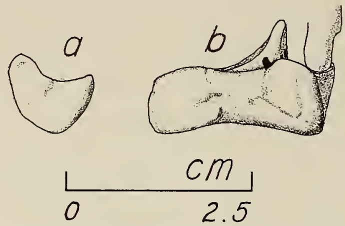

Fig. 2. *Coelophysis bauri*. a, internal view, dorsal process not shown; b, anterior view, of left astragalocalcaneum and distal end of fibula. AMNH block 5. × 1.

index of 65. The dorsal process has a bearing surface 3 mm wide that underlies a flange of the tibia, and dips 20° medially. There is a shallow upper horizontal groove across the anterior face separating the condyles from the dorsal process. This groove ends laterally in a notch in the calcaneum. Just above this groove, and 5 mm medial to the fibular edge, a 2 mm foramen marks the opening of a canal which penetrates laterodistally into the bone. The body of the astragalus

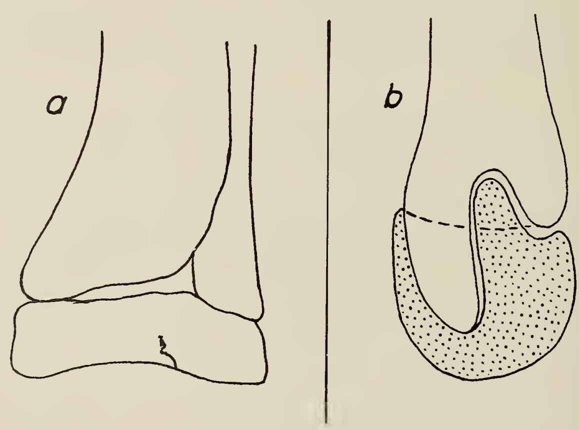

Fig. 3.
Syntarsus rhodesiensis, left tarsus in a, anterior; b, section through centre, anterior to right. From Raath 1969, fig. 6, approximately × 1,75.

is but 4 mm thick laterally below the tibia. Its medial edge slopes 45° postero-laterally. The posterior edge is sharp and rounds upward about 4 mm so that the astragalocalcaneum forms the entire bearing condyle. The calcaneum is fused, is 8 mm deep below the fibula and forms the lateral part of the condyle.

Syntarsus rhodesiensis Raath, 1969, from near the top of the Forest Sandstone of Rhodesia (equivalent to the upper Red Beds of the Stormberg Series, of Norian age), is a small theropod with an astragalocalcaneum but 20 mm wide and 9,7 mm high, an H:B index of 49. This is a very low, almost incipient dorsal process, the slope of its medial surface but 12°. However, the cross section of the right tarsus given by Raath shows that the ascending process continues up into the tibia and is covered anteriorly by an overlap of the tibia. The true H:B index is therefore somewhat greater than 49. The general structure of this tarsus, with its low, deeply set dorsal process seems to us to be ceratosauroid, although it should be noted that Galton (1971: 788) considers the ankle to be 'typically sauropodomorph'.

Young (1951: 75, fig. 15) describes a theropod astragalocalcaneum (no. V 73) from the Dark Red Beds of Haungchiatien, the uppermost beds of the Lower Lufeng Series, generally considered to be upper Norian to Rhaetic. This is a gigantic bone, 157 mm broad, with a total height of 84 mm, an H:B index of 53. The slope of the dorsal process is 18° and it begins at the lateral

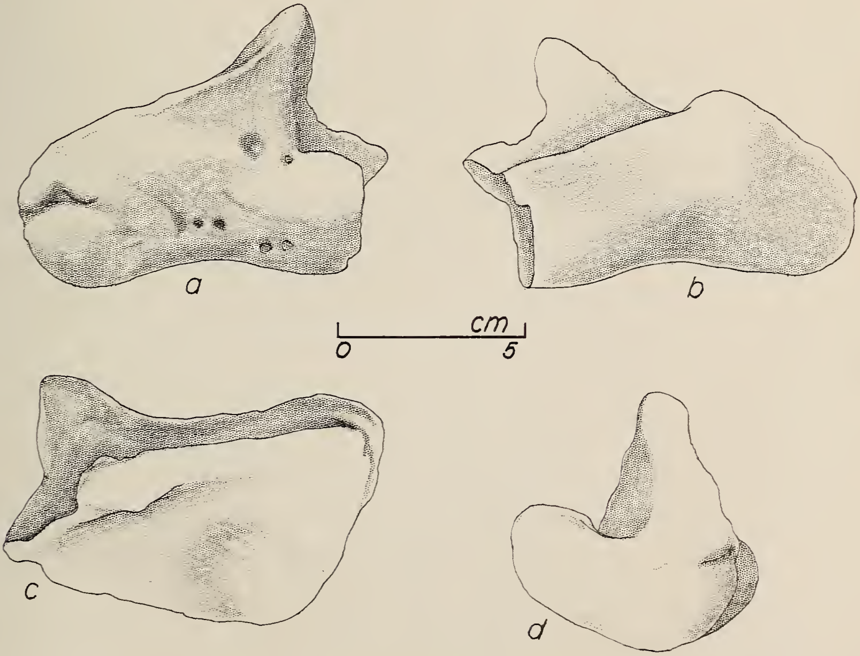

Fig. 4. Ceratosauroid from Lufeng Beds.
Left astragalocalcaneum in a, anterior; b, posterior; c, dorsal; d, medial views. From Young 1951, fig. 15. × ¼.

border and is almost straight. The fusion of the two bones and the medial extent of the dorsal process are not allosauroid but are similar to *Dilophosaurus* and *Ceratosaurus*.

Halticosaurus liliensterni (Knollenmergel, Norian, of Thuringia) has a primitive astragalus, with the calcaneum solidly fused into an astragalocalcaneum. The two bones are 79 mm wide anteriorly, the astragalus 65 mm. The dorsal process is 42 mm high and dips medially 11°, the H:B index is 65. The dorsal

Fig. 5. *Halticosaurus liliensterni*, type.
Anterior view of left astragalus and distal end of tibia.
× ½.

process is thick (16 mm) and in lateral view the entire element, including the dorsal process, is almost circular, measuring 46 mm anteroposteriorly.

The type of *Dilophosaurus wetherilli* (UCMP 37302) has an astragalus 91 mm broad anteriorly and but 76 mm broad posteriorly. In anterior view the dorsal process is 70 mm high above a straight line across the base (H:B index 76), 14 mm thick at mid-height, and shows little if any bearing surface. It begins at the median border and rises in a uniform slope of 16° to about 20 mm from the summit where the slope increases to give a total slope of 27°. The anterior condylar surface is concave transversely, and rounds below into a medial condyle and a lateral condyle that continues onto the calcaneum. There is a slight transverse groove in the centre of the rounded medial edge. The anterodorsal border of this surface projects forward and is separated from the dorsal process by a broad upper horizontal groove that deepens laterally and terminates at the fibular socket. The rounded anterolateral projection of the astragalus forms the anterior border of the fibular socket. About half of this socket is in the astragalus. A rounded buttress runs down the anterolateral corner of the dorsal process and extends onto the anterolateral projection of the lateral condyle. In dorsal view the sulcus for the tibia runs posterolaterally, and a small boss in the posterior border, towards the medial edge, fits into a socket in the tibia. The tibial sulcus does not extend behind that for the fibula, as it does in *Allosaurus*, indicating that the distal end of the tibia lacks the great

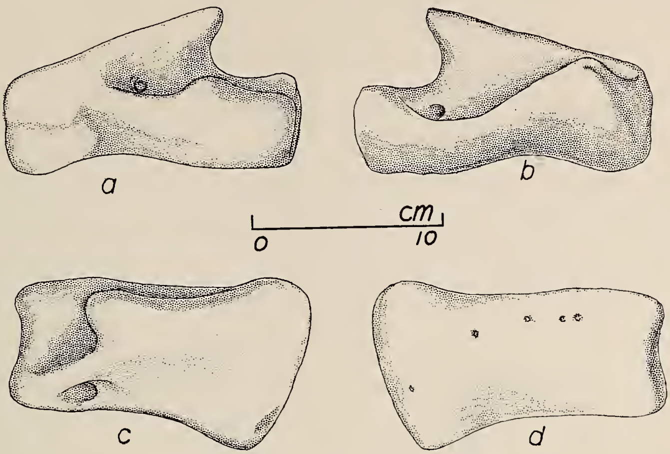

Fig. 6. *Dilophosaurus wetherilli*, type.
Left astragalus in a, anterior; b, posterior; c, dorsal; d, ventral views. UCMP 37302. × ½.

lateral expansion of the latter, as is shown by the tibia itself. The socket for the fibula is 17 mm broad in front and wedges out posteriorly, its bearing surface increasingly taken over by the calcaneum. In medial view the bone is very thick beneath the tibia, contrasting strongly with the thin bone of *Allosaurus*. In posterior view the lateral edge is sharp, but it thickens medially to form a posteromedial knob. A sharp ridge runs down posterolaterally from the dorsal process to project above and behind the calcaneum, and to divide the tibial sulcus from that for the fibula. There is a pit near the base of the dorsal process, probably for ligaments binding the astragalus to the tibia. The medial surface of the dorsal tip of the dorsal process is a flattened surface 14 mm wide that faces toward the anteromedial corner. The ventral surface of the astragalus is saddle-shaped, convex anteroposteriorly and concave laterally. It forms a lateral and a medial condyle, constricted between. Its lateral and medial edges converge posteriorly, the former sharp and forming a straight suture with the calcaneum. The medial edge is rounded. In lateral view the socket for the fibula is 30 mm above the distal end, 10 mm higher than that for the tibia. The surface for the calcaneum is subcrescentic, slightly concave, with a triangular projection overhanging the calcaneum near the posterior edge.

The isolated right tarsus of another specimen (UCMP 37303) also from the base of Kayenta Formation of Arizona (late Triassic or early Jurassic) has the calcaneum solidly in place and the total breadth is estimated to be 114 mm. The dorsal process has been crushed down somewhat by the anterolateral shoulder of the tibia and it is but 55 mm high, an H:B index of 48.

In the right tarsus of the type of *Ceratosaurus nasicornis*, from the late Jurassic

Morrison Formation of Colorado USNM 4735 *fide* Gilmore (1920: 111, fig. 65) the two proximal tarsalia are fused into an astragalocalcaneum and the dorsal process of the astragalus is quite restricted. In anterior view the dorsomedial border slopes upward rather regularly from the inner base instead of beginning part way laterally as in *Allosaurus*—a difference noted by Gilmore. There is a triangular area above the lateral border of the astragalus and below the tibia and fibula which does not seem to have been filled by the dorsal process. This triangle is evident on the right and left type tarsi and also on two others at the University of Utah. This area seems to be ossified differently from the rest of the bone and could possibly have been occupied by calcified cartilage. The lateral end of the tightly fused calcaneum is deeply concave. The left tibia and astragalocalcaneum of this same individual, YPM 4681, has a breadth of 118 mm and an H:B index of 45, and is similar to

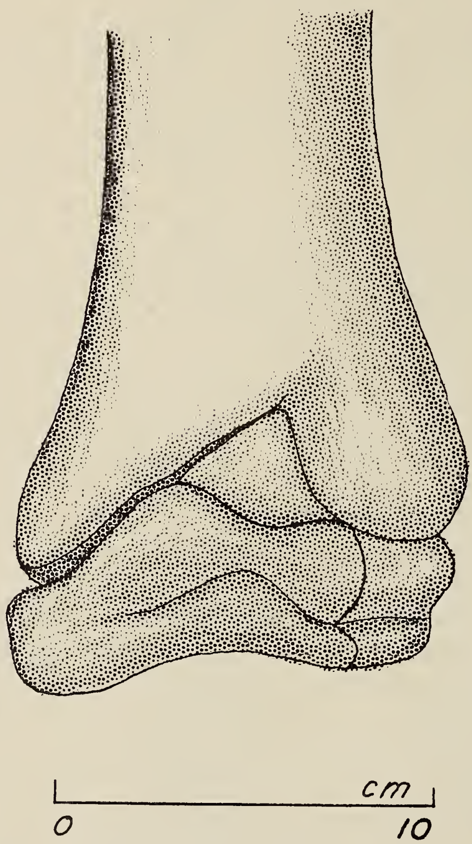

Fig. 7. *Ceratosaurus nasicornis*, type.
Anterior view of left astragalocalcaneum and distal end of tibia, YPM 4681. The rest of this skeleton is at the United States National Museum. × ½.

that of the left side. On both right and left the suture between astragalus and calcaneum is visible on the anterior face.

A fine right tibia and tarsus at the University of Utah (UUVP 5682), referable to the genus *Ceratosaurus*, if not the type species, has a breadth of 147 mm and an H:B index of 49. A second associated specimen (UUVP 5681), the largest known, has a breadth of 175 mm and an H:B index of 42.

Huene (1933: 56, pl. 19, fig. 1) describes an astragalus that he identifies as allosaurid, from the Lameta beds (Turonian) of Jubbulpore. This astragalus (K27/684) is incomplete medially and is described as thick laterally and very thin, almost platelike in all other parts. It is 50 mm anteroposteriorly, with the dorsal process 20 mm high and 30 mm broad. It is 'twisted in the direction of the transverse axis'. Huene gives no reasons for identifying this as allosaurid and his illustrations do not support his view. His 'dorsal view', fig. 1a, is, with the tibia vertical, evidently posterodorsal with the dorsal process down. The ligamentary pit is near the base of the dorsal process. Figure 1b, an anterior view, shows a low dorsal process with an external vertical ridge curving ventromedially from the summit. The lateral face of the tibial sulcus rises into a high wall behind the sulcus. The lateral view shows a smooth calcaneal face. All of these features contrast with those of the allosauroids and are much more ceratosauroid. An isolated calcaneum is also ceratosauroid in being broad and parallel-sided.

THE ALLOSAUROID TARSUS

Phillips (1871: 214) describes an astragalus as that of *Megalosaurus bucklandi*. It rises upward in a broad flat plate which fits in a well-defined hollow in the flattened anterior face of the tibia. Its lateral extension toward the fibula is cut off by a nearly vertical surface for the calcaneum. Phillips makes no mention of an interdigitation of calcaneus and astragalus, but the dorsal process and bulbous medial condyle are of the general allosauroid pattern. We therefore consider this a possible early allosauroid pending further investigation. It is presumably from the Oxford Clay.

Deslongchamps (1838, pl. 6, fig. 12) described and illustrated the astragalus of his *Poecilopleuron bucklandi*. This specimen was formerly at Caen but Dr Donald Russell informs us that it was destroyed during the war. It came from Vesulian or Lower Bathonian rocks, approximately equivalent to the Stonesfield deposits. The astragalus is large, its breadth 148 mm and the H:B index is 75. The medial edge of the dorsal process begins rather far laterally, and slopes upward at about 60°. The medial half is low, the condyle gently convex transversely. The lateral face for the calcaneum is concave dorsoventrally and is much the thickest part of the body. The astragalus is advanced in the height of the dorsal process and its lateral restriction. The shape and position of the dorsal process, and the free medial condyle, are allosauroid but there does not seem to have been any interdigitation of astragalus and calcaneum. It could be a primitive representative of this group.

Eustreptospondylus oxoniensis Walker, 1964 (UMOJ 13558), is from the Middle Oxford Clay (Upper Callovian) of Wolverton, southern England. The astragalus is separate from the calcaneum and measures 87 mm broad and 62 mm high, an H:B index of 71. The right astragalus

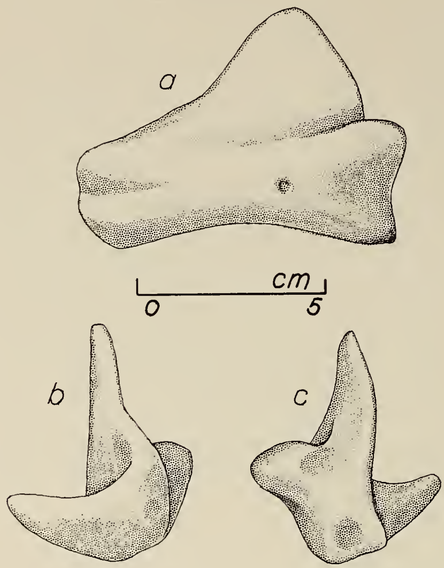

Fig. 8. *Eustreptospondylus oxoniensis*, type.
Right astragalus (reversed to left) in a, anterior; b, medial; c, lateral views. × ½.

was sketched by Huene (1926, fig. 36) and he also illustrated the separate calcaneum, since lost. A detailed drawing sent us by Mr H. P. Powell allows us to make a more complete description. It has a breadth of 87 mm and a height of 62 mm, an H:B index of 71. The anterior view shows a 33° slope of the medial edge of the dorsal process. This edge is concave and slopes but 26° at the base. It has a long, low, rounded medial condyle and a fairly sharp ventrolateral border of the lateral condyle. The dorsal edge of the calcaneal border is set forward of the dorsal process and has a rounded dorsolateral projection. The dorsal process is separated from the anterior surface by an upper horizontal groove that fades out medially. There is no deep pit for a process of the calcaneum as in *Allosaurus*, but there is a concave edge for the calcaneum. A slight lower horizontal groove runs about a quarter of the way inward from the centre of the medial condyle. The lateral view shows a high calcaneal facet with the upper horizontal groove at the base of the dorsal process separating the rounded anterodorsal projection. The posterior foot below the tibia is bluntly rounded behind and becomes longer anteroposteriorly on the inner side. The striking features of this view are the strong posterodorsal projection above the lateral condyle and the upper horizontal groove above and behind it.

The medial view shows a rather thick (high) medial condyle that is 43 mm anteroposteriorly on the right astragalus and 48 mm on the left. The foot is rounded posteriorly. The general shape of the dorsal process and its upper horizontal groove, and the bulbous medial condyle are allosauroid, but the deep interdigitation of the astragalus and calcaneum found in *Allosaurus* has not developed.

The famous Honfleur specimen described by Cuvier (1836, 10:204, pl. 249, figs 34–36) in his 4th edition, and probably earlier, was stated to have come from one of the two blue marls above the Caen stone. Huene (1926: 38) places the horizon as Upper Callovian. It consists of the right astragalus and the distal end of the tibia. The taxonomic problems arising out of this and the other Honfleur material are very difficult and need not concern us here, but Walker (1964: 122) reviewed them and referred this specimen to his *Eustreptospondylus divesensis*. Cuvier's original description was inadequate for our comparisons, and he used a different orientation. The specimen was well illustrated by Piveteau (1923: 9, pl. 4, figs 4, 5). One of us (Welles) was privileged to examine this specimen at Paris and noted that the tibia had a sharp bend in the supra-astragalar shelf and no real bearing surface. The astragalus had a breadth of 115 mm and a height of 94 mm, a H:B index of 82. In anterior view the dorsal process is evidently nearly entire, its tip of 2 mm finished in plaster, and is broad and rounded above. Its inner edge is concave, the slope 30°. The upper horizontal groove is very weak, present laterally but fading out medially, and there is a strong dorsolateral process above the lateral condyle, widely separate from the dorsal process. The lower horizontal groove is very poorly developed. In dorsal view the sulcus for the tibia is very narrow laterally and there is no development of a projection to insert in the tibia. In lateral view the calcaneal facet is a vertical oval with a fibular sulcus 41 mm above the base. In posterior view the posterior edge is sharp laterally but thickens medially. In general features this astragalus is allosauroid, but much more primitive than *Allosaurus*. In addition to the astragalus, Cuvier (pl. 249, fig. 38) illustrates a bone that he identifies as a tarsal bone. This is evidently an allosauroid calcaneum in that it has a central projection below the fibular facet. There is no proof that the two bones are from the same individual, but if they are, this is the earliest known occurrence of the pattern found in *Allosaurus*, consisting of separate though interlocked astragalus and calcaneum.

An astragalus at Yale (YPM 1252) from the Morrison Formation at Como Bluff is possibly referable to *Coelurus agilis*. In anterior view it is 74 mm broad and 58 mm high, an H:B index of 78. It has a vertical lateral base to the dorsal process and an inner border that slopes about 68°. The dorsal process is confined to the lateral half and there is a broad upper horizontal groove at the lateral base of the dorsal process. This groove separates a posterodorsal projection of the lateral condyle from the dorsal process. The posterior face shows a ligamentary pit at the centre of the base of the dorsal process. The body is deepest medially, about the same depth below the ligamentary pit, and thinnest laterally. The sulcus for the distal end of the tibia is divided into halves, the inner half sloping slightly medially (3°) and the lateral half rather steeply (10°) laterally. All of these features are of a general allosauroid nature.

A cast of a large specimen of *Allosaurus fragilis* from the Upper Morrison Formation of central Utah sent us by Professor James H. Madsen, Jr., of the University of Utah, has a maximum breadth of 185 mm along the anteroventral border, a posterior breadth of 160 mm, and a height of 160 mm. The H:B index is 87. (The specimen illustrated by Gilmore (1920, fig. 50, USNM 7336) has a breadth of 200 mm and a height of 170 mm, an H:B index of 85.) In anterior view the dorsal process begins 67 mm lateral to the inner edge and rises at a steep slope (53°) to the summit. This slope is interrupted by a dorsal bulge near the top. A strip along the lateral border, its widest part

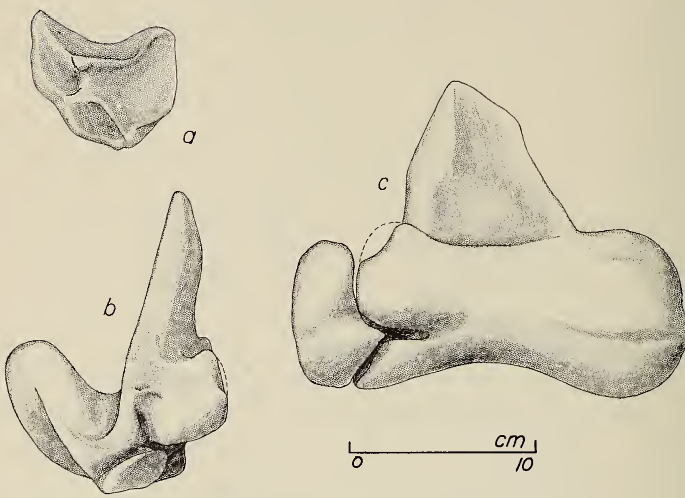

Fig. 9. *Allosaurus fragilis*, cast of right astragalus and calcaneum from University of Utah.
a, internal view of calcaneum; b, lateral view of astragalus; c, anterior view of both. × $\frac{1}{4}$.

30 mm, is set at an angle of 35° to the anterior face, and forms a plane surface for the fibula. The upper horizontal groove, along the base of the dorsal process, is deep and rounds posterolaterally into the sulcus for the fibula. This groove is deepest laterally and ends medially at the base of the dorsal process. The dorsal process is broad, flat, and thin, extending laterally and not excavated by the fibular socket. The lower horizontal groove is pronounced and extends laterally for half the width of the astragalus. The lateral edge, against the calcaneum, has a deep notch that received a point of the calcaneum. In posterior view the ligament pit at the base of the dorsal process is large and deep. The lateral half forms a fairly thin (20 mm) floor below the tibial sulcus and has a sharp posterior edge. The medial half thickens, both upward and downward, to form a bulbous medial condyle rising 70 mm above the base. Behind this

condyle the floor of the tibial sulcus is 42 mm thick. This floor is obscured by the upturned posterior edge, but the medial 70 mm makes an angle of 17° with the outer 110 mm. In dorsal view the sulcus for the distal end of the tibia is 83 mm broad medially and but 32 mm broad laterally. In lateral view the socket for the distal end of the fibula is set into the astragalus between the dorsal process and the anterodorsal knob above the lateral condyle. This inset is a continuation of the upper horizontal groove. Below and behind the fibular sulcus is a complex notch for the calcaneum, and although not fused, the two bones are deeply interlocked. In addition to the deep notch in the centre of the astragalus below the fibular socket there are two rounded processes which project into sockets in the calcaneum. One of these processes is anterodorsal, the other ventral, and this complex interdigitation of the notch and two processes prevents any movement between astragalus and calcaneum. The socket for the fibula is high above that for the tibia. (A specimen illustrated by Gilmore (1920, fig. 48, USNM 4734) is pathologic in having a crushed, and evidently healed, distal end of the fibula that lowered the calcaneum about half its height. This same specimen was illustrated by Marsh (1896, pl. 11) with the distortion corrected.) In ventral view the astragalus is distinctive in that it narrows laterally to about half of its medial anteroposterior dimension. The medial border is at nearly right angles to the posterior border but makes only a 55° angle with the anterior border. The lateral border is rounded, but the notch for the process of the calcaneum is evident.

The calcaneum of *Allosaurus* has its medial face modified to match the astragalus. There is a central projection that carries the floor of the fibular socket into the astragalus. Anteroventral to this is a socket that receives the anterodorsal projection of the astragalus, and posteroventral to this is another socket facing ventromedially, below and anteromedial to the tibial sulcus. This socket receives the ventral projection of the astragalus. The posteromedial face of the calcaneum is a concave semilunar sulcus for the lateral edge of the tibia. The lateral face is also semilunar with its upper concavity forming the outer rim of the fibular socket. The calcaneum is larger than in ornithomimoids or albertosauroids, but smaller than in ceratosauroids.

Another *Allosaurus* astragalar cast, representing a small, immature individual, was also sent to us by Professor James J. Madsen, Jr. This specimen is particularly interesting in that it has an H:B index of 104, much greater than the 87 of the large cast. The dorsal process also differs from the adult in that the inner edge begins to slope up gently at 22° from the inner border, then, about half-way out the dip increases gradually to about 72°.

THE ALBERTOSAUROID TARSUS

Gilmore (1933: 38, fig. 10) describes the astragalus and calcaneum of *Alectrosaurus olseni* from the Iren Dabasu Formation (Cenomanian) of Mongolia. This is his second specimen, AMNH 6554. Gilmore designated this and the fore limb from 30,5 m away (AMNH 6368) cotypes yet treated them as representing two individuals. To avoid confusion we here designate this specimen, AMNH 6554, the type of the species. The fore limb therefore becomes a referred specimen. The tibia and tarsus were seen by Gilmore to be closest to *Albertosaurus libratus* (which he called *Gorgosaurus sternbergi*). He also noted the difference in the proportion of the dorsal process of the astragalus in the two species, rising $\frac{1}{3}$ of the height of the tibia plus astragalus in *A. libratus* while it is $\frac{1}{4}$ in *Alectrosaurus olseni*. The height of the astragalus is given as 180 mm and measurements taken from the illustration give an estimated breadth of 120 mm, an H:B index of 150. The medial edge of this specimen is missing but enough is present to show the deep upper horizontal groove. The lateral part shows a slight ventrolateral buttress against the lateral condyle, weaker than in *Albertosaurus arctunguis*, but stronger than in *A. sarcophagus*. The calcaneum is more strongly developed and has a higher anteromedial process than in *A. arctunguis*.

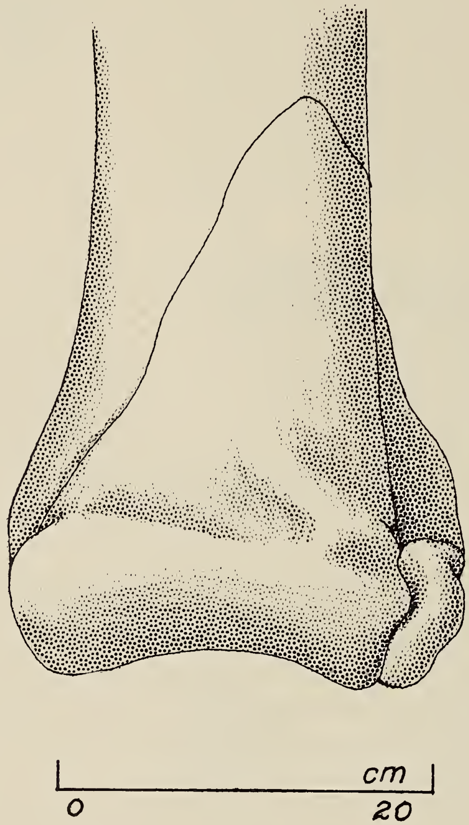

Fig. 10. *Albertosaurus libratus*, type. Anterior view of left tarsus and distal end of tibia, from Lambe 1917, fig. 42. × $\frac{1}{4}$.

Lambe (1917: 69, fig. 42) described and figured the tibia and tarsus of *Gorgosaurus libratus* from the Belly River Formation (Judith River, Campanian) of Alberta. This was placed in the genus *Albertosaurus* by Russell (1970: 4). The dorsal process of the astragalus is nearly as broad as the base and the inner face of the base is 'flat or only slightly concave'. The dorsal process is set back from the body and separated by a deep upper horizontal groove which is very deep at the centre. The height of the astragalus, taken from the figure, is 314 mm, the breadth 212 mm, an H:B index of 148. The laterodistal buttress against the top of the lateral condyle is rather strongly developed, not so pronounced as in *A. sarcophagus*, referred (= *A. arctunguis*), but more so than in either *A. sarcophagus*, referred (= *Dryptosaurus incrassatus*, referred, Lambe 1904) or *Alectrosaurus olseni*. The calcaneum is also intermediate in its stage of reduction between *A. olseni* and *Albertosaurus* '*arctunguis*'.

Parks (1928: 29, fig. 12) described the astragalus of *Albertosaurus arctunguis* from the Horseshoe Canyon Formation (Campanian-Maastrichtian) of Alberta. This was placed in synonymy with *A. sarcophagus* by Russell (1970: 4). It has the calcaneum in place, although probably not fused because it is free in the specimen described as *Dryptosaurus incrassatus* (Cope) by Lambe (1904: 20, pl. 6, fig. 6), later referred to *A. sarcophagus* by Osborn (1905: 263). The breadth of the combined astragalus and calcaneum is 265 mm, that of the astragalus 216 mm (from the illustration). Parks notes 'no significant difference between' this astragalus and that ascribed by Lambe to *A. sarcophagus*, except that the dorsal process is a little wider and the body a little thicker. However, a comparison of the two illustrations shows a considerable difference in the shallowness of the body, the deep narrow anterior concavity, and especially the development of the large rounded ventrolateral buttress onto the lateral condyle in *A. arctunguis*. Although the two species have astragali developed on the same basic principles, that of *A. arctunguis* is more specialized.

Lambe (1904: 20, pl. 6, figs 6–8) illustrated and described an astragalus and the distal end of a tibia as *Dryptosaurus incrassatus* (Cope). This was referred to *Albertosaurus sarcophagus* by Osborn (1905: 265), and is from the Horseshoe Canyon Formation (Campanian-Maastrichtian) of Alberta. Russell (1970: 10) identified this as NMC 5601. The breadth is given as 248 mm and an estimate of the height is 241 mm, an H:B index of 97. The dorsal process is set laterally about 30 mm, its lateral edge rising steeply at first, then sloping more gently at about 52°. In anterior view this astragalus has a large medial condyle that is 86 mm high. The central constriction is roughened by vertical grooves and ridges. The condylar body is separated from the dorsal process by a deep upper horizontal groove that is deepest in the centre. The surface for the calcaneum is notched anteroventrally and this surface is described as a concave area. The medial and lateral ends of the bone are oblique, a common feature that makes the posterior border narrower than the anterior. The calcaneum is said to have contributed only to the support of the fibula.

Cope (1866: 316; 1870: 105, pl. 9, fig. 3) described the astragalus of his

Laelaps aquilunguis from the Barnsboro marl pits of Gloucester Co., New Jersey. The generic name was preoccupied and Marsh (1877: 88) proposed *Dryptosaurus* to replace it. The horizon is the Greensand Navesink Formation, of Maastrichtian age (Miller 1962: 195). Cope's figures show an astragalus that underlies only the anterior half of the tibia and has a very peculiar dorsal process. This is probably a badly eroded specimen and should be restored along the lines of *Albertosaurus*. This would make the dorsal process at least 50% higher than the breadth of the astragalus. It would make the peculiar opening near the lateral base into the lateral, eroded edge of the upper horizontal groove. The ventral posterior projection below the tibia should be somewhat increased. So restored, the astragalus has a breadth of 184 mm. The ventrolateral buttress does not reach the calcanear surface and its development is between that of *Albertosaurus libratus* and *A. arctunguis*. The facet for the calcaneum indicates that the calcaneum was nearly as reduced as in the latter species. This, therefore, seems to be an albertosauroid astragalus.

An astragalus from an incomplete skeleton collected in the Hell Creek Formation (Maastrichtian) of Garfield Co., Montana in the Los Angeles County Museum collections (LACM 23849) kindly lent us by Dr Ralph Molnar is badly broken, but the lateral and medial ends are preserved along with the base of the dorsal process. It can be restored with confidence, except for the dorsal process, with a breadth of 196 mm. In anterior view the dorsal process arises 17 mm late-

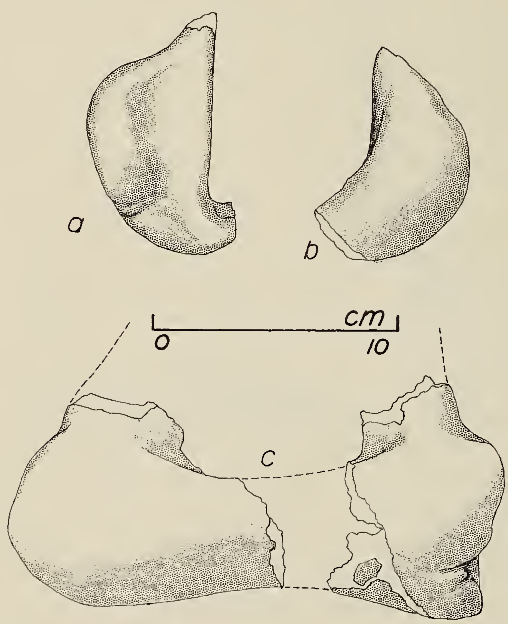

Fig. 11. Albertosauroid astragalus (right, reversed) from the Hell Creek Beds.

a, lateral; b, medial; c, anterior views. LACM 23849. × $\frac{1}{3}$.

rally from the bulbous medial condyle. The upper horizontal groove at the base of the process is shallow medially and laterally, so was probably not very deep centrally. A 5 mm perforation enters the body of the bone at the lateral end of the groove. The tunnel from this perforation leads ventromedially. The ventrolateral buttress is weak and rounds gently into the lateral condyle. In ventral view the condyles are smoothly rounded and not marked by the lower horizontal groove that in *Allosaurus* separates a distal face from an anterior face. The medial condyle is very large, bulbous, and smoothly rounded, somewhat like that of *Dryptosaurus*, except that the lower posterior edge slants more steeply anterolaterally. The lateral condyle is also round, yet has a flattening of the anteroventral face. The lateral condyle has a narrow cleft near the base, in the same position as that of *Allosaurus*, but very much smaller. No such cleft is evident in *Dryptosaurus*.

THE ORNITHOMIMOID TARSUS

The astragalus of the partial skeleton from the late Jurassic Tendaguru beds referred to *Elaphrosaurus bambergi* by Janensch (1925: 41, pl. 6, fig. 1) is 88 mm broad and 56 mm anteroposteriorly. The condyles are nearly equal and are separated by a gentle constriction. The condylar surface ends posteriorly in a sharp, straight edge. In anterior view the bone is pinched in between the condyles. There is a dorsolateral projection that is separated from the dorsal process by the upper horizontal groove, which runs across the front of the bone. Janensch describes a dorsomedial projection in front of this groove which is a triangular process about 13 mm high. The dorsal process is described as weakly developed and near the medial edge, yet its height is indicated by an 85 mm high sulcus on the anterior face of the tibia. From this we estimate an H:B index of 100. In dorsal view the tibial sulcus is divided by a central rise. Its lateral half narrows and also has a concavity for the fibula. We have not examined this specimen but Janensch's description indicates that it is the only theropod astragalus with a dorsomedial process in front of the upper horizontal groove. Janensch considers the entire bone to be astragalus, yet he describes a suture near the lateral edge which sets off a small dorsally-narrowed surface that he thought must be the calcaneum. If the astragalocalcaneum is shifted to its proper position on the ventral face of the tibia, we find that the lateral part is in the proper position for a calcaneum, and that the resulting calcaneum is rather large. This is considerably advanced over the coelophysoid type and the height of the dorsal process excludes it from the ceratosauroids. It lacks the ventrolateral buttress of the albertosauroids and seems to represent a primitive ornithomimoid.

Ostrom (1970: 75, pl. 13, figs D, E) described his *Microvenator celer* from the Cloverly Formation of Montana (Aptian-Albian) as having the astragalus extending the full breadth of the tibia with a small recess for a tiny, chiplike calcaneum. The breadth is 22,3 mm, the height 42,3 mm so the H:B index is 190, the highest known. The dip of the inner margin of the high dorsal process is

75°. This is certainly an advanced tarsus of the ornithomimoid pattern, to be expected in a form of Aptian-Albian age.

Stenonychosaurus inequalis Sternberg, from the Judith River Formation was figured by Russell (1969 fig. 11). The tibia and astragalus of the type specimen is broken some 65 mm up the shaft so the dorsal extent of the astragalus is not known. It shows an astragalus very much like that of *Microvenator* but the inner condyle slants more medially and the lateral condyle is more nearly vertical.

Lydekker (1891, pl. 5, fig. 2) described the tibia of a small theropod from the Wealden of the Isle of Wight, BMNH R186. This he referred to *Calamosaurus foxi*. There are no tarsal bones associated with this tibia but the area for articulation of the dorsal process of the astragalus is an acute triangle, indicating a high dorsal process with an estimated H:B index of 132.

Ostrom (1969: 120, fig. 68) described the astragalus and calcaneum of his *Deinonychus antirrhopus* from the Cloverly Formation of south-central Montana. The two bones were not fused, nor were they fused to the tibia. The astragalus is described as similar to that of *Ornithomimus* (YPM 542) but larger and more perfectly rounded distally. This distal rounding is extreme, given by Ostrom as 155° to 180° of arc, and evidently continued by the tibia to approximately 200°, providing an 'unusual extension of the foot'. The breadth is 59 mm and the H:B index at least 142. The dorsal process is very thin and at least 84 mm high. It rises about 5 mm from the medial edge at a steep angle of 72° and is very broad (52 mm) at the base, extending laterally behind the calcaneum. The tibial sulcus is carried laterally onto the posterior face of the calcaneum behind the high, small fibular sulcus. This tarsus is ornithomimoid in its extremely high dorsal process, but is aberrant in retaining so large a calcaneum.

Gilmore (1920: 138) describes the astragalus that he considers to be a cotype of *Ornithomimus affinis*, from the Arundel Formation, Lower Cretaceous of Maryland. This is 78 mm broad, the dorsal process much eroded to a height of 56 mm, and is narrow anteroposteriorly. Russell (1972: 379) transfers this species to the genus *Archaeornithomimus*.

Lambe (1902: 50, fig. 11) described the right hind limb of *Ornithomimus altus* from the Judith River Formation, (Russell 1972: 383), Red Deer River, Alberta. This was referred to the genus *Struthiomimus* by Osborn (1917: 744). From the illustration the astragalus is 129 mm wide and 224 mm high, an H:B index of 174. The dorsal process lies along the fibular side of the tibia, the lower border of each concave, with the tibia expanding rapidly distally. Lambe does not describe this bone in detail, but later (1904: 20) notes that the medial and lateral ends are less oblique than in *Dryptosaurus incrassatus* (referred specimen). He also states that the astragalus does not coalesce with the tibia. The calcaneum has an upper sulcus for the fibula and 'one behind to aid the astragalus in supporting the tibia'.

Ornithomimus velox was figured by Marsh (1890, pl. 1, fig. 1), as from the *Ceratops* beds of Colorado, the Denver Formation, Maastrichtian (Russell 1972: 379). The astragalus is 52 mm broad and 80 mm high, an H:B index of

154. The calcaneum is very thin and Marsh did not state whether it was fused or not. If fused, the astragalocalcaneum had a breadth of 65 mm. This is an

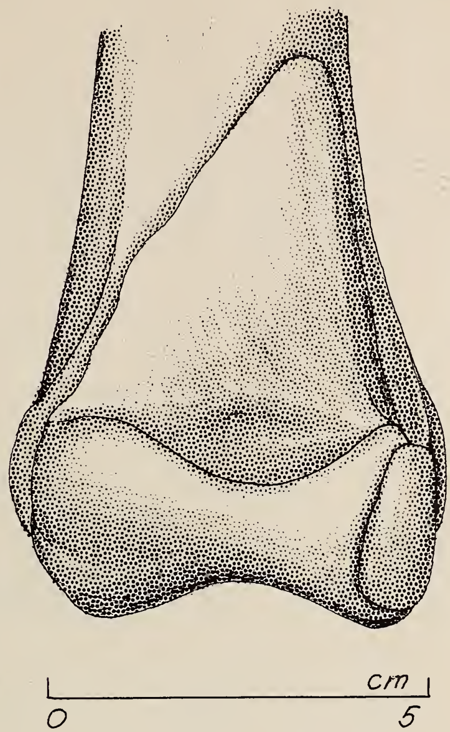

Fig. 12. *Ornithomimus velox*, type. Anterior view of distal end of left tibia and tarsus, from Marsh 1890, pl. 1, fig. 1. × 1.

extremely specialized tarsus in that the calcaneum is so reduced that there was little or no support for the fibula, and this, in turn, must have been greatly reduced. These features were noted by Marsh, who likened it to the ostrich tarsus. The dorsal process is extremely high, its lateral edge nearly vertical and its medial edge dipping 67° near the base, the total angle of dip being 60°. Another specialization of this tarsus is seen in ventral view where the astragalus does not completely cover the lower end of the tibia, but the tibia forms a narrow rim of bearing surface along the posterior edge and wraps around the medial edge of the astragalus. This narrow tibial rim also extends laterally behind the calcaneum.

THE TYRANNOSAUROID TARSUS

The astragalus of *Tyrannosaurus rex*, from the Hell Creek beds of Montana, was illustrated by Osborn (1917, pl. 25) as about 425 mm broad and 530 mm high, an H:B index of 125. However, in the archives of the American Museum of Natural History we found a detailed unpublished illustration by Erwin S. Christman, which was probably done under the supervision of Osborn or Barnum Brown. This differs drastically from Osborn's illustration and it evidently represents an entirely different kind of astragalus. It therefore seems likely to us that Osborn's illustration was based on *Allosaurus*. We made a thorough search for the specimen, and although we failed to locate it we feel that Christman's drawing is authentic. It bears the same number (AMNH 5027) as the beautiful skull from the Hell Creek Formation of Montana collected by Brown in 1907. The locality is the east side of Big Dry, 13 km from Willis Ranch, 40 km south of Lisman, Mont., top of basal ss., 24 m above the Fox

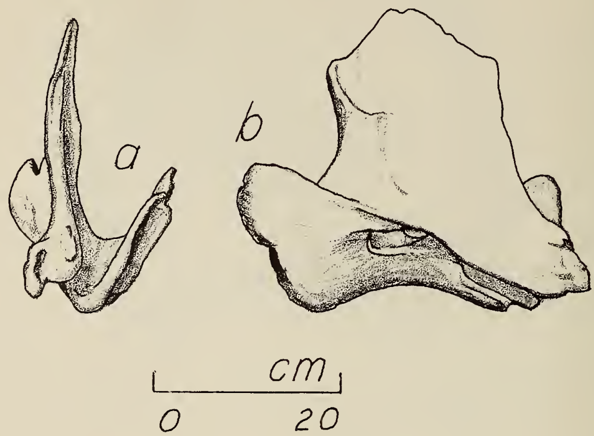

Fig. 13. *Tyrannosaurus rex*. Left astragalus in a, lateral view; b, anterior view. Redrawn from unpublished illustration by Erwin S. Christman. AMNH 5027. × ¼.

Hills. From Christman's illustration the anterior view shows a breadth of 372 mm and a height of 320 mm, yielding an H:B index of 86. The dorsal process is broad and is distinctive in that the medial edge slants dorsomedially and is concave. The lateral edge slopes ventrolaterally and ends above the pit for the calcaneum. The upper horizontal groove is but weakly developed medially and is entirely absent laterally where the dorsal process rounds gently into the lateral condyle. The medial condyle is 160 mm high, protrudes dorsomedially, and its upper edge slopes ventrolaterally to form a shelf above a groove (? the lower horizontal groove) which ends by rounding back and down into the lateral condyle 60 mm internal to the calcaneal border. At about the centre of the astragalus, just below the shelf is a large (68 × 28) horizontal foramen that opens into the tibial sulcus. In lateral view the edge of the dorsal process is rounded and does not seem to have formed the usual flat surface for the fibula. The lateral condyle is low, rounding gently into the dorsal process without the separation of an upper horizontal groove. An open vertical groove could be for either the fibula or the calcaneum, probably the latter. The posterior process is very thin, with its edge high (172 mm) above the condyle. The trough for the tibia is very narrow laterally where it descends to within 20 mm of the base. It broadens medially, as with most theropod astragali.

Summary

In reviewing this study of the theropod astragali, the ceratosauroids develop a low, thick dorsal process which is sunk into the tibia. The calcaneum is large and may be free or fused. This tarsus undergoes little change from late Triassic to late Cretaceous and does not seem to have given rise to any other line. The allosauroids have a moderately high dorsal process which is confined to the lateral half of the tibial surface. The medial condyle is large and rounded. The calcaneum is large and free, and in *Allosaurus* is deeply interdigitated with the astragalus. The time range is Middle Jurassic through late Jurassic. The albertosauroid astragalus has a high, broad dorsal process with a deep upper horizontal groove at its anterior base. This groove is interrupted laterally by a ventrolateral buttress to the lateral condyle. There is no lower horizontal groove and the calcaneum becomes very small and is loosely attached to the astragalus. This kind of tarsus is found throughout the late Cretaceous. The ornithomimoid astragalus develops an extremely high and very thin dorsal process that overlies the face of the tibia without being deeply inset. Distally it is equal to the tibia in breadth. The upper horizontal groove at the anterior base of the dorsal process is strongly arched ventrally and there is no lower horizontal groove. The calcaneum becomes extremely reduced and may be lost. The time range is late Jurassic to late Cretaceous. The tyrannosauroid tarsus only appears in the latest Cretaceous in a single known form. The astragalus bears a high, wide dorsal process as in other late Cretaceous theropods, but it differs in numerous other characters and appears to indicate a separate origin from known Cretaceous forms.

It is obvious that there has been a general tendency among theropods to increase the height of the dorsal process of the astragalus. The ceratosauroids seem to have minimized this tendency, the ornithomimoids to have maximized it. Whether or not this tendency can be used as an indicator of geologic age, as was attempted by Welles (1954: 597), can only be determined by additional specimens and further study.

This survey suggests some tentative relationships based on a very few specimens. Many undescribed astragali are known, and when they are studied we will have a much more solid basis for our conclusions.

Acknowledgements

We should like to thank Professor James H. Madsen, Jr., Department of Geology and Geophysics, University of Utah; Professor John H. Ostrom, Yale Peabody Museum; Dr Rudolph Daber, Museum für Paläontologie, Museum für Naturkunde; Dr E. H. Colbert, Museum of Northern Arizona; and Dr P. Taquet, Institut de Paléontologie, Muséum National d'Histoire Naturelle for permission to study and photograph specimens. Dr Ralph Molnar, Los Angeles County Museum, sent us the Hell Creek astragalus. We are especially indebted to Mr H. P. Powell of the University Museum, Oxford, for his drawings of *Eustreptospondylus*. Dr Eugene Gaffney of the American Museum of Natural History allowed us to use the unpublished illustration of *Tyrannosaurus*. The illustrations are by Mr David Cook, staff artist of the University of California Museum of Paleontology, except Figures 2 and 13 which are by Welles.

Postscript

Upon the receipt of page proof we note the subsequent papers that include descriptions of theropod tarsi which have not been included in our survey:

Bider, A., Demay, L. & Thomel, G. 1972. *Compsognathus corallestris*, nouvelle espèce de dinosaurien théropode du Portlandien de Canjuers (Sud-Est de la France). *Annls Mus. Hist. nat. Nice* **1** (1): 9–40.

Osmólska, H., Roniewicz, E. & Barsbold, R. 1972. A new dinosaur, *Gallimimus bullatus* n. gen., n. sp. (*Ornithomimidae*) from the Upper Cretaceous of Mongolia. *In*: kielan-jaworowska, Z., *ed.* Results of the Polish-Mongolian Palaeontological Expeditions. IV. *Palaeont. pol.* **27**: 103–143.

The tarsi of *Compsognathus corallestris* and *Gallimimus bullatus* display numerous characters which undoubtedly place them in our ornithomimoid group.

It should also be noted that Cruickshank has recently described the tarsus of the *Lystrosaurus* zone thecodont *Proterosuchus* which is 'almost identical to that of an eosuchian'. The calcaneum has a well-developed tuber.

(Cruickshank, A. R. I. 1972. The proterosuchian thecodonts. *In:* joysey, k.a. & kemp, t. s., *eds. Studies in vertebrate evolution*: 89–119. Edinburgh: Oliver & Boyd.)

Also Bonaparte has described the astragalus of an indeterminate saurischian from the upper Los Colorados Formation (Norian), of La Rioja, Argentina. This is a very primitive astragalus with only an incipient dorsal process and its relationship to theropod tarsi is uncertain.

(Bonaparte, J. 1971. Los tetrápodos del sector superior de la Formacion Lós Colorados, La Rioja, Argentina. (Triásico Superior.) I Parte. *Op. lilloana* **22**: 1–185.

References

Broom, R. 1921. On the structure of the reptilian tarsus. *Proc. zool. Soc. Lond.* **1921**: 143–155.

Cope, E. D. 1866. [Remarks on *Laelaps*.] *Proc. Acad. nat. Sci. Philad.* **1866**: 316–317.

Cope, E. D. 1870. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Trans. Am. phil. Soc.* (n.s.) **14**: i–viii, 252. [This is a corrected reprint of Cope 1869, and is a second preprint of the whole volume, which was issued in 1871 without further changes]

Cuvier, G. 1836. *Recherches sur les ossemens fossiles, ou l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces*. 4th ed. **9**, **10**. Paris: D'Ocagne.

Deslongchamps, J. 1838. Mémoire sur le *Poekilopleuron bucklandi*, grand saurien fossile, intermédiare entre les crocodiles et les lézards. *Mém. Soc. linn. Normandie* **6**: 37–146.

Ewer, R. T. 1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. *Phil. Trans. R. Soc.* (B) **248**: 379–435.

Galton, P. M. 1971. The prosauropod dinosaur *Ammosaurus*, the crocodile *Protoschus*, and their bearing on the age of the Navajo Sandstone of northeastern Arizona. *J. Paleont.* **45**: 781–795.

GEGENBAUR, C. 1864. *Untersuchungen zur vergleichenden Anatomie der Wirbelthiere.* Erstes Heft. Carpus und Tarsus. Leipzig: Engelmann.

GILMORE, C. W. 1920. Osteology of the carniverous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bull. U.S. natn. Mus.* **110**: 1–154.

GILMORE, C. W. 1933. On the dinosaurian fauna of the Iren Dabasu formation. *Bull. Am. Mus. nat. Hist.* **67**: 23–78.

GREGORY, W. K. & CAMP, C. L. 1918. Studies in comparative myology and osteology. III. *Bull. Am. Mus. nat. Hist.* **38**: 447–563.

HUENE, F. VON. 1926. The carnivorous Saurischia in the Jura and Cretaceous formations principally in Europe. *Revta Mus. La Plata* **29**: 35–167.

HUENE, F. VON. 1933. Sub-Order: Carnosauria. *In*: HUENE, F. VON & MATLEY, C.A. The Cretaceous Saurischia and Ornithischia of the Central Provinces of India. *Mem. geol. Surv. India Palaeont. indica* (n.s.) **21**: 41–59.

JANENSCH, W. 1925. Wissenschaftliche Ergebnisse der Tendaguru-Expedition 1909–1912. Die Coelurosaurier und Theropoden der Tendaguruschichten Deutsch-Ostafrikas. *Palaeontographica* Suppl. **7** (1. Reihe, Teil 1, Lief. 2): 1–99.

KREBS, B. 1963. Bau und Function des Tarsus eines Pseudosuchiers aus der Trias des Monte San Giorgio (Kanton Tessin, Schweiz). *Palaeont. Z.* **37**: 88–95.

LAMBE, L. M. 1902. New genera and species from the Belly River series (Mid-Cretaceous). *In:* OSBORN, H. F. & LAMBE, L. M. On Vertebrata of the Mid-Cretaceous of the North West Territory. *Contr. Can. Palaeont.* **3** (2): 23–81.

LAMBE, L. M. 1904. On *Dryptosaurus incrassatus* (Cope) from the Edmonton series of the North-West Territory. *Contr. Can. Palaeont.* **3** (3): 1–27.

LAMBE, L. M. 1917. The Cretaceous theropodous dinosaur *Gorgosaurus*. *Mem. geol. Surv. Brch Can.* **100**: 1–84.

LYDEKKER, R. 1891. On certain ornithosaurian and dinosaurian remains. *Q. Jl geol. Soc. Lond.* **47**: 41–44.

MARSH, O. C. 1877. Notice of a new and gigantic dinosaur. *Am. J. Sci.* (3) **14**: 87–88.

MARSH, O. C. 1890. Description of a new dinosaurian reptile. *Am. J. Sci.* (3) **39**: 81–86.

MARSH, O. C. 1896. The dinosaurs of North America. *Rep. U.S. geol. Surv.* **16** (1): 133–414.

MATTHEW W. D. & BROWN, B. 1923. Preliminary notices of skeletons and skulls of Deinodontidae from the Cretaceous of Alberta. *Am. Mus. Novit.* **89**: 1–10.

OSBORN, H. F. 1917. Skeletal adaptations of *Ornitholestes, Struthiomimus, Tyrannosaurus*. *Bull. Am. Mus. nat. Hist.* **35**: 733–771.

OSTROM, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bull. Peabody Mus. nat. Hist.* **30**: 1–165.

OSTROM, J. H. 1970. Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana. *Bull. Peabody Mus. nat. Hist.* **35**: i–vii, 1–234.

PARKS, W. A. 1928. *Albertosaurus arctunguis*, a new species of theropodous dinosaur from the Edmonton Formation of Alberta. *Univ. Toronto Stud. geol. Ser.* **25**: 1–42.

PEABODY, F. E. 1951. The origin of the astragalus of reptiles. *Evolution* **5**: 339–344.

PHILLIPS, J. 1871. *Geology of Oxford and the valley of the Thames.* Oxford: Clarendon Press.

PIVETEAU, J. 1923. L'arrière-crâne d'un dinosaurien carnivore de l'Oxfordien de Dives. *Annls Paléont.* **12**: 1–11.

RAATH, M. A. 1969. A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. *Arnoldia* (*Rhodesia*) **4** (28): 1–25.

RABL, C. 1910. *Bausteine zu einer Theorie der Extremitäten der Wirbeltiere.* 1 Teil. Leipzig: Engelmann.

ROMER, A. S. 1971. The Chañares (Argentina) Triassic reptile fauna. X. Two new but incompletely known long-limbed pseudosuchians. *Breviora* **378**: 1–10.

ROMER, A. S. 1972. The Chañares (Argentina) Triassic reptile fauna. XV. Further remains of the thecodonts *Lagerpeton* and *Lagosuchus*. *Breviora* **394**: 1–7.

RUSSELL, D. A. 1969. A new specimen of *Stenonychosaurus* from the Oldman Formation (Cretaceous) of Alberta. *Can. J. Earth Sci.* **6**: 595–612.

RUSSELL, D. A. 1970. Tyrannosaurs from the Late Cretaceous of western Canada. *Publs Palaeont. natn. Mus. nat. Sci.* (*Can.*) **1**: v–viii, 1–34.

SCHAEFFER, B. 1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. *Bull. Am. Mus. nat. Hist.* **78**: 395–472.

Walker, A. D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Phil. Trans. R. Soc.* (B) **248**: 53–135.
Welles, S. P. 1954. New Jurassic dinosaur from the Kayenta Formation of Arizona. *Bull. geol. Soc. Am.* **65**: 591–598.
Young, C. C. 1951. The Lufeng saurischian fauna in China. *Palaeont. sin.* (n.s.): **13**: 1–96.
Young, C. C. 1964. The pseudosuchians in China. *Palaeont. sin.* (C) **19**: 105–205.